CHAPTER 2

Breeding, Genetics, and Cultivar Development

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2.1 Introduction

The potato is widely grown worldwide and ranks first in production among vegetable crops. Its popularity is due to its high yield, nutritional quality, and broad array of culinary uses. Until the early 1900s, potato breeders grew seed from open-pollinated fruits, which likely resulted from a mixture of self- and cross-pollination. They inevitably selected for day-length adaptation, disease resistance, and high yield. In addition, they probably also selected for compact plants, large tubers, and smooth tuber shape. These breeding goals are similar to those of modern potato breeders. However, breeders today must also consider processing traits and, increasingly, nutritional quality. During the past 150 years, potato breeders have developed cultivars with earlier maturity, smoother tubers, and improved processing quality (Douches et al., 1996; Love et al., 1998). However, it is a surprise to note that total yield has not improved over time.

2.2 The Germplasm Resource

Wild *Solanum* species are found in 16 countries, from the southwestern United States to central Chile (Figure 2.1) (Spooner and Salas, 2006). The greatest diversity of species is found in central Mexico at 20°N, and in the southern hemisphere, especially in the highlands of the Andes between 8° and 20°S (Hijmans and Spooner, 2001). Wild potatoes grow from sea level to 4300 m, but are most commonly found at altitudes of 2000–4000 m. Collectively, these species represent a more diverse and accessible germplasm resource than in any other crop (Ross, 1986; Hanneman, 1989; Peloquin et al., 1989; Hawkes, 1990). Wild species are adapted to a much wider range of habitats than the cultivated potato. They are found in a tremendously diverse array of environments, including the cold high grasslands of the Andes, hot semi-desert and seasonally dry habitats, humid subtropical to temperate mountain rainforests, cultivated fields, and even as epiphytes in trees (Figure 2.2) (Hawkes, 1990; Hijmans et al., 2002). These wild species contain genes encoding numerous traits not found in cultivars and represent an especially rich source of disease-resistance and tuber-quality genes (Hanneman, 1989; Spooner and Bamberg,

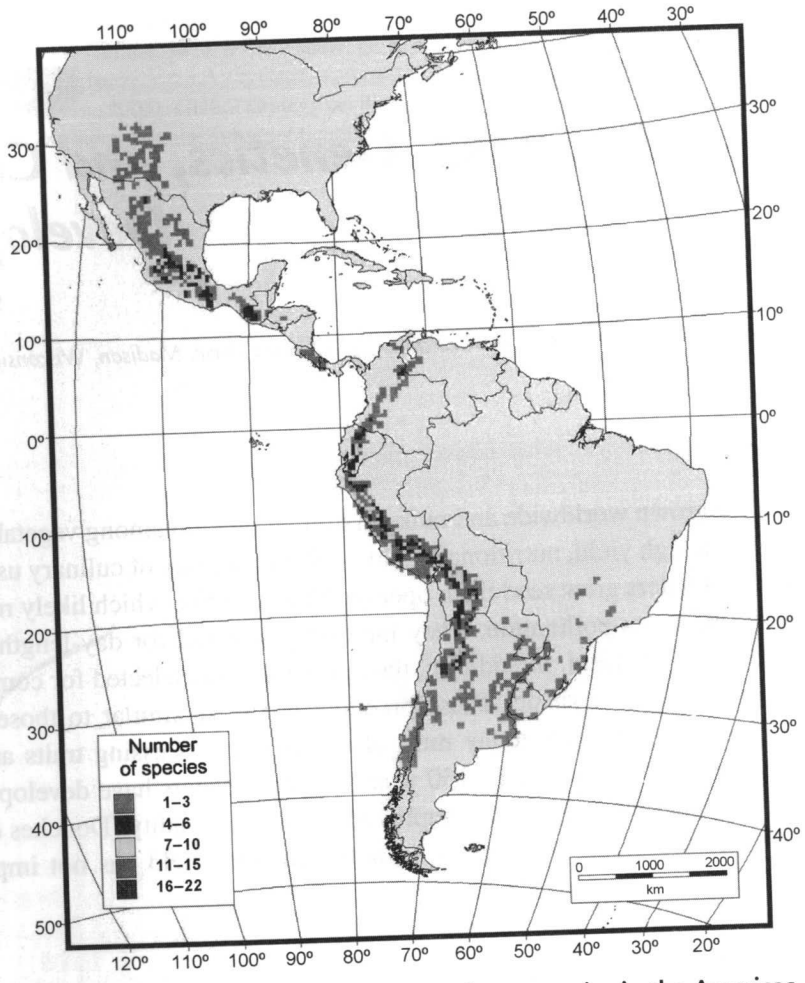

Figure 2.1: The distribution of wild *Solanum* species in the Americas.

1994; Jansky, 2000). About 64% of wild *Solanum* species are diploid ($2x = 24$), with most of the remaining species tetraploid ($4x = 48$) or hexaploid ($6x = 72$) (Hijmans et al., 2007).

The wild and cultivated relatives of potato are extensively represented in gene banks throughout the world. Potato gene banks include the International Potato Center (CIP, Lima, Perú), United States Potato Introduction Project (NRSP-6, Sturgeon Bay, Wisconsin,USA), Dutch German Potato Collection (CGN, Wageningen, The Netherlands and BGRC, Braunschweig, Germany), Institute of Plant Genetics and Crop Plant Research (GLKS, Gross Luessewitz, Germany), Commonwealth Potato Collection (CPC, Dundee, Scotland), N.I. Vavilov Institute (VIR, St. Petersburg, Russia), and the Instituto Nacional de Tecnología Agropecuaria (INTA, Balcarce, Argentina).

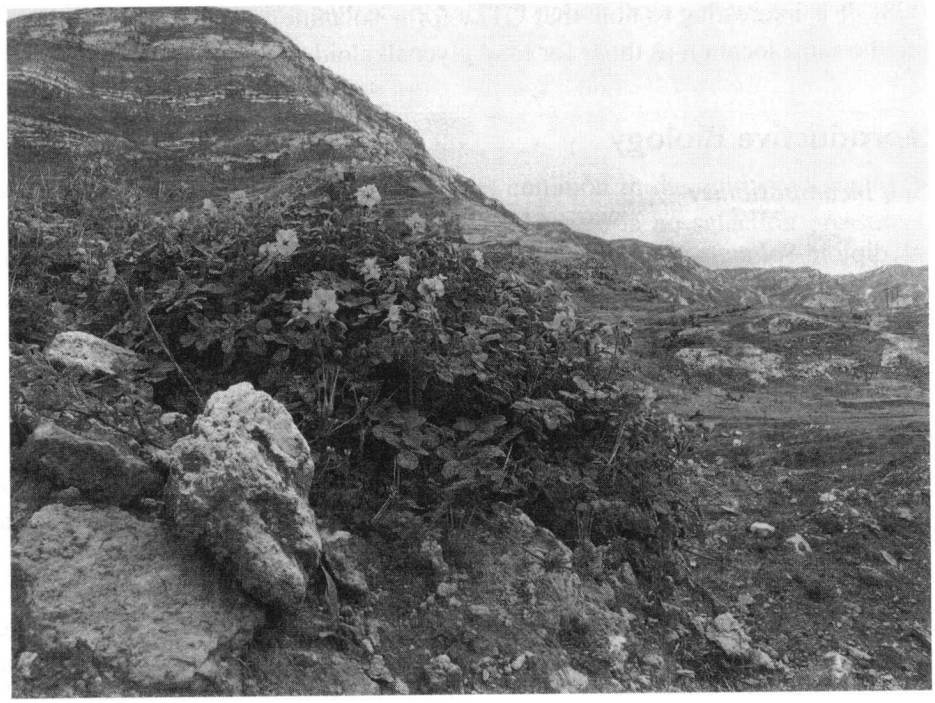

Figure 2.2: A wild *Solanum* species (*S. bukasovii*) in its native habitat in the Andean highlands.

In disease and tuber-quality screening studies, significant variation exists among accessions within a species and even among plants within an accession. Therefore, while a species may be characterized as resistant to cold sweetening, for example, it is important to realize that not every plant in that species carries that trait. A fine screening evaluation must be used, in which individuals within resistant accessions are screened and then the most resistant individuals are maintained clonally for use by breeders (Bamberg et al., 1996; Douches et al., 2001; Jansky et al., 2006; Zlesak and Thill, 2004; Jansky et al., 2008).

The cultivated potato contains low levels of glycoalkaloids, typically solanine and chaconine, which are bitter and can be toxic at high levels. High levels of glycoalkaloids were selected against during the domestication of potato (Johns and Alonso, 1990). However, wild potato species may contain high levels of glycoalkaloids, some of which are not found in the cultivated potato (Friedman, 2006). It is important, therefore, for breeders to continue to monitor glycoalkaloid levels in tubers when wild species have been introgressed into the cultivated potato. Because a number of glycoalkaloids are produced by complex biochemical pathways in potato, QTL analysis has been employed to elucidate the genetic control of this trait. Major QTLs have been identified on several chromosomes (Yencho et al., 1998). Chromosome I seems to be an especially important source of genes involved in controlling glycoalkaloid levels (Sørensen

et al., 2008). It is interesting to note that QTLs for α-solanine and α-chaconine content were mapped to the same location as those for total glycoalkaloid content.

2.3 Reproductive Biology

2.3.1 Self incompatibility

Almost all diploid *Solanum* species are self-incompatible due to a gametophytically controlled system (Swaminathan and Howard, 1953; Pandey, 1962; Cipar et al., 1964). A highly polymorphic locus, called the *S* gene, expressed in pollen tubes as they grow through the style, prevents the fertilization of an egg cell by a sperm cell of the same genotype. The style produces an S-RNase that prevents the normal growth of genetically matching pollen tubes (Luu et al., 2000). Therefore, attempts to self-pollinate most wild diploid *Solanum* species fail. On the other hand, polyploids, including potato cultivars, are capable of self-fertilization. The pistil is capable of inhibiting pollen, but pollen tubes are incapable of eliciting an incompatibility reaction (Levin, 1983).

Genetic systems that overcome self-incompatibility in diploid potatoes have been reported in two germplasm sources. Hybrids between cultivated diploid potatoes and an *S. tuberosum* haploid (US-W4) were reported to be self-compatible due to the action of a dominant self-incompatibility inhibitor in US-W4 (De Jong and Rowe, 1971). Three generations of selfed individuals were generated. A dominant self-incompatibility inhibitor (*Sli*) has been reported in the wild diploid species *S. chacoense* (chc) (Hosaka and Hanneman, 1998a, c). This gene has been mapped to the distal end of chromosome 12 (Hosaka and Hanneman, 1998b). The *Sli* gene is independent of the *S* locus, which maps to chromosome 1 (Tanksley and Loaiza-Figueroa, 1985). The *Sli* gene has been transferred to a number of diploid genotypes, allowing them to be self-pollinated (Phumichai et al., 2006).

2.3.2 Unilateral incompatibility

Unilateral incompatibility is a phenomenon in which self-compatible species can be crossed as a female, but not as a male, to self-incompatible species (Abdalla and Hermsen, 1972). Pollen tubes fail to penetrate stylar tissue in self-incompatible (female) X self-compatible (male) crosses. Although most diploid *Solanum* species are self-incompatible, the Mexican species *S. verrucosum* is self-compatible. Dinu et al. (2005) found that *S. verrucosum* could be crossed as a female, but not as a male, to self-incompatible species. It is sometimes possible to find exceptional plants that do not exhibit unilateral incompatibility in self-incompatible X self-compatible interspecific crosses (Pandey, 1962). The identification of such plants allows a breeder to overcome the unilateral incompatibility crossing barrier. For example, exceptional plants ('acceptors') that accept *S. verrucosum* pollen and produce fertile hybrids have been reported (Eijlander et al., 2000). It is interesting that some 'acceptor' plants will accept pollen

of any *S. verrucosum* plant, while others only accept pollen from certain *S. verrucosum* plants (Hermsen 1978).

2.3.3 Male sterility

Male sterility due to deleterious nuclear genes is common in the cultivated potato (Howard, 1970). Because the marketable product is not seed, there is no selection pressure for high fertility in breeding programs. In fact, fruit development may partition resources away from tuber yield, so breeders may inadvertently select against high fertility (Jansky and Thompson, 1990). In addition, deleterious recessive alleles can accumulate in tetraploid potato cultivars because they are more easily masked than in diploids.

Potato also exhibits male sterility due to interactions between cytoplasmic genes and nuclear genes. Cytoplasmic-genetic male sterility has been reported in a number of interspecific hybrids (Dionne, 1961a, b; Grun et al., 1962; Grun and Aubertin, 1966; Grun, 1970; Abdalla and Hermsen, 1973; Hermundstad and Peloquin, 1985b; Tucci et al., 1996; Santini et al., 2000; Phumichai and Hosaka, 2006). For example, crosses between Chilotanum Group haploids and cultivated Andigenum Group clones produce male fertile hybrids when the haploids are the male parent, but male sterile hybrids when the haploids are the female parent (Grun et al., 1962; Ross et al., 1964; Carroll, 1975).

Levels of cytoplasmic genetic male sterility are frequently variable, presumably due to genetic and environmental influences (Hanneman and Peloquin, 1981). Breeders can, therefore, overcome this type of sterility by either carrying out reciprocal crosses or selecting parents that do not contain sensitive cytoplasm or dominant nuclear sterility genes (Iwanaga et al., 1991; Tucci et al., 1996). In addition, fertility restorer genes may be identified. For example, there is a dominant gene (*Rf*) that restores fertility to plants that contain the dominant male sterility gene (*Ms*) in the presence of sensitive cytoplasm (Iwanaga et al., 1991). Selection of Chilotanum Group haploids carrying the *Rf* gene allows for the production of male fertile offspring even when the male parent contains the dominant male sterility gene *Ms*. Tucci et al. (1996) also identified a male fertility restorer gene in a haploid X *S. chacoense* hybrid.

2.3.4 2n gametes

Most polyploid crop plants originated from the union of numerically unreduced (2n) gametes. These gametes are produced in plants carrying meiotic mutations. These mutations interrupt meiosis so that gametes contain the parental (sporophytic) chromosome number rather than half that number. These meiotic mutations occur naturally and frequently in cultivated and wild potatoes (Peloquin et al., 1999; Carputo et al., 2000a). Some meiotic mutations result in the production of 2n eggs (Stelly and Peloquin, 1986b; Werner and Peloquin, 1991a), while others produce 2n pollen (Quinn et al., 1974; Mok and Peloquin, 1975b). As discussed later, a cross

between a tetraploid and a 2n gamete-producing diploid will produce tetraploid offspring. 2n pollen is easily detected microscopically because diploid pollen grains are larger than monoploid pollen grains (Quinn et al., 1974). 2n eggs can also be detected microscopically via a stain clearing technique (Stelly et al., 1984), but this is a laborious procedure and not practical for large-scale screening. Diploid clones that produce 2n eggs can be identified by simply crossing them as females to tetraploids (Erazzú and Camadro, 2007). If seeds are produced, then 2n eggs were present in the diploid parent.

The cytological change that results from a meiotic mutation produces dramatic genetic consequences. Normally, in anthers, the four products of meiosis are separated so that their poles define a tetrahedron. Cytokinesis then produces four haploid microspores. In contrast, one type of meiotic mutant called parallel spindles produces two microspores, each with an unreduced (sporophytic) chromosome number. The first division is normal, but in the second division, the spindles are parallel. When cytokinesis follows, two diploid microspores are produced. Even though the first meiotic division occurs in this mutant, the genetic result of parallel spindles is equivalent to first division restitution (FDR) because gametes contain non-sister chromatids from the centromere to the first crossover. The parallel spindles genotype exhibits variable expressivity and incomplete penetrance (Mok and Peloquin, 1975a). Consequently, not all gametes of a mutant plant are 2n, and not all plants carrying the mutation produce 2n pollen. While the genetic consequence of 2n pollen formation in potato is typically FDR, that of 2n egg formation is second division restitution (Stelly and Peloquin, 1986a; Werner and Peloquin, 1990). Second division restitution gametes contain sister chromatids from the centromere to the first crossover.

The genetic consequences of FDR 2n gametes are very different from those of SDR 2n gametes. In an FDR 2n gamete, all loci from the centromere to the first crossover on each chromosome have the same genetic constitution as the parent of that gamete. That is, all dominance (intralocus) interactions up to the first crossover are maintained in the gametes (Figure 2.3). Even in the chromosomal region beyond the first crossover, half of the loci that were heterozygous in the parent will remain so in 2n gametes. Since potato chromosomes are small, there is typically only one crossover per chromosome (Yeh et al., 1964). Consequently, FDR 2n gametes provide a unique and powerful method of transmitting blocks of advantageous dominance (intralocus) and epistatic (interlocus) interactions to polyploid offspring even following meiosis, which usually breaks up such interactions. In contrast, SDR 2n gametes contain non-sister chromatids from the centromere to the first crossover. While FDR 2n gametes transmit 80% of the diploid parent heterozygosity to tetraploid offspring, SDR 2n gametes transmit less than 40% (Peloquin, 1983).

2.3.5 Endosperm Balance Number

In angiosperms, double fertilization results in the production of an embryo and endosperm, both of which are critical for the development of viable seed. Diploid plants produce diploid embryos and triploid endosperm tissue. The endosperm contains two genomes of the maternal parent and

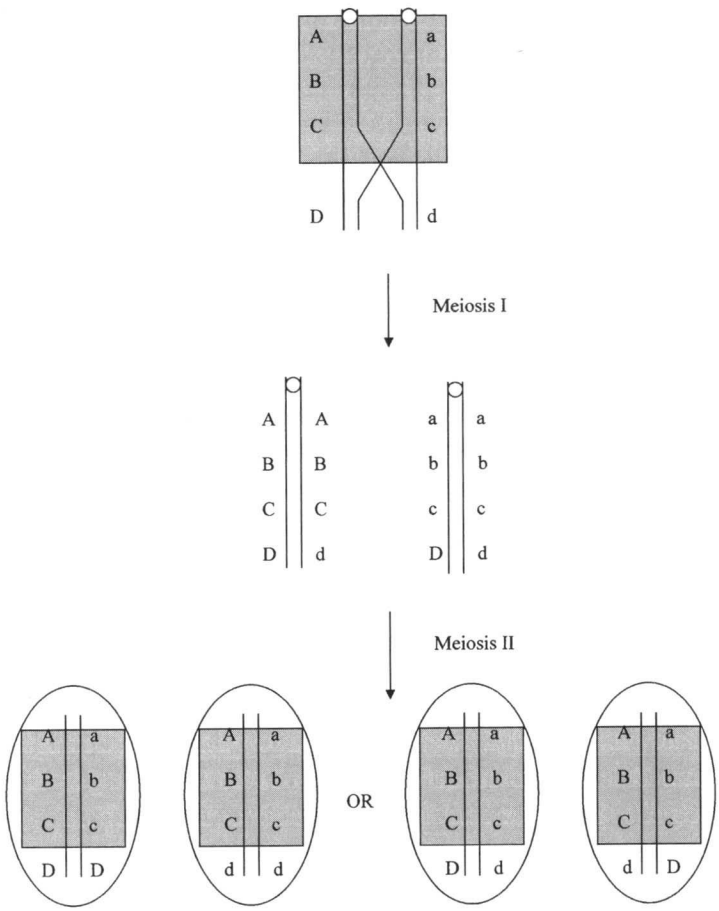

Figure 2.3: All genetic interactions from the centromere to the first crossover are transmitted to offspring in gametes produced by a first division restitution mechanism such as parallel spindles.

one genome of the paternal parent. Intraspecific intraploidy crosses in potato typically produce viable seeds containing well-developed endosperm. Conversely, in most interploidy crosses, inviable seeds are produced due to endosperm failure (Brink and Cooper, 1947). However, endosperm may also fail to develop adequately in some intraploidy, interspecific crosses, while some interploidy crosses succeed. A 2:1 maternal:paternal ratio of endosperm balance factors, rather than genomes, is necessary for normal endosperm development in potato (Johnston et al., 1980). The nature of these endosperm balance factors has yet to be elucidated, although genetic models have been proposed (Ehlenfeldt and Hanneman, 1988; Camadro and Masuelli, 1995). *Solanum* species have been assigned endosperm balance numbers (EBN) based on their ability to hybridize with each other (Hanneman, 1994). Barring other crossing barriers, viable seeds will be produced from crosses between plants with matching EBN values. This will produce a

2:1 maternal:paternal ratio of endosperm balance factors after fertilization of the central cell to produce endosperm. The most common ploidy, EBN combinations in potato are 6x (4EBN), 4x (4EBN), 4x (2EBN), 2x (2EBN) and 2x (1EBN).

Breeders use EBN values to determine whether interspecific crosses will succeed. The EBN concept also allows them to design strategies to access wild germplasm by manipulating EBN (Johnston et al., 1980). Endosperm balance number can be increased through somatic doubling (Ross et al., 1967; Sonnino et al., 1988) or the production of 2n gametes. Endosperm balance number can be reduced through anther culture or parthenogenesis (discussed below).

An example will serve to illustrate the value of the EBN concept to access wild *Solanum* germplasm. Triploid hybrids were formed between the Mexican 4x (2EBN) species *S. stoloniferum* and 2x (2EBN) cultivated diploids, both of which were selected for 2n gamete production (Brown, 1988). These triploid plants produced fertile 2n (3x, 2 EBN) pollen, allowing them to be crossed onto 4x (4EBN; gametes 2 EBN) cultivated potato clones (Brown and Adiwilaga, 1990). The majority of offspring were pentaploid, as expected if the functional pollen grains from the triploid parent were numerically unreduced (2n). The advantage of producing triploids rather than hexaploids in this cross is that homoeologous chromosome pairing (between the two species) is more likely to occur in triploids, increasing opportunities for introgression of chromosomal segments of the wild species into the cultivated genome.

It is important to note that, while knowledge of EBN and 2n gamete production allows for successful cross prediction most of the time, there are exceptions. Sometimes intra-EBN crosses fail and, at other times, inter-EBN crosses succeed even without the presence of 2n gametes. EBN is only one component of a complex system of pre- and post-zygotic interspecific crossing barriers (Masuelli and Camadro, 1997; Chen et al., 2004).

2.3.6 Haploids

Haploids are sporophytes with the gametophytic chromosome number. Haploids (2x) of tetraploid potato cultivars provide a mechanism for direct gene transfer from wild 2x relatives and allow breeders to work at the diploid level. As discussed below, selection progress is more rapid with diploids than tetraploids. Haploids can also be used to measure the genetic load in the tetraploids from which they are derived, since deleterious alleles hidden in tetraploids are often expressed in haploids.

Haploids can be produced from tetraploid cultivars and breeding clones via parthenogenesis (Hougas and Peloquin, 1957). When a tetraploid is crossed with any of several selected diploid clones, some of the offspring are diploid. In these crosses, both sperm cells from the pollinator enter the central cell, allowing normal endosperm to develop. This stimulates the division of the egg cell in the absence of fertilization, resulting in the production of a haploid (2x) embryo

(von Wangenheim et al., 1960; Montelongo-Escobedo and Rowe, 1969; Peloquin et al., 1996). Sometimes, functional 2n pollen in the pollinator produces tetraploid offspring. It is important to distinguish between seeds that resulted from fertilization of the egg cell by 2n pollen (which would be tetraploid and undesirable) and those that were not (and are therefore haploids). The pollinators are homozygous for a dominant seed spot marker, so seeds expressing the marker are discarded and those lacking the marker are retained with the expectation that they are haploids (Peloquin and Hougas, 1959; Hermsen and Verdenius, 1973).

Populations of haploids provide unique opportunities for the genetic analysis of polygenic traits. A population of haploids from a single highly heterozygous tetraploid clone represents a random pool of female gametes. Genetic analyses can be carried out on this population without the confounding effects of fertilization. In addition, genetic variability hidden in polyploids can be revealed in populations of haploids (Peloquin et al., 1991). As a result of segregation, haploids may express traits that were not found in their tetraploid parents. Haploid populations have been used to characterize the genetic basis of total tuber yield, average tuber weight, tuber number, dry matter content, tuber dormancy, vine maturity, and tuber glucose levels (Kotch et al., 1992).

Breeders usually select haploid parents based on traits useful for the generation of hybrids (fertility, vigor, profuse flowering) and for the ability to produce offspring with high-quality tubers (Yerk and Peloquin, 1990b; Werner and Peloquin, 1991b). Genetic variation among haploids for plant and tuber traits is common and has been widely reported (Peloquin and Hougas, 1960; DeMaine, 1984; Matsubayashi, 1979; Rousselle-Bourgeois and Rousselle, 1992; Hutten et al., 1995b). Disease resistance traits are also variable among haploids, with some haploid clones exhibiting better resistance than their parents. Haploids with resistance to Verticillium wilt, soft rot, common scab, blackleg, potato virus X, and potato cyst nematode have been reported (Hutten et al., 1995b; Carputo et al., 1996; Jansky et al., 2003; Ercolano et al., 2004).

Tetraploid potatoes are typically more vigorous and higher yielding than their haploid offspring (Peloquin and Hougas, 1960; DeMaine, 1984; Kotch 1987). The loss of vigor and yield in haploids is due to ploidy reduction and inbreeding depression. The magnitude of this loss at the diploid level differs depending on the tetraploid clone from which the haploids were derived (Kotch, 1987).

Potato monoploids (1x) can be produced from diploids via anther culture (Veilleux et al., 1985) or pollination (Uijtewaal et al., 1987). While the production of monoploids through anther culture is possible, it can be difficult because it requires the presence of genes for androgenic competence ('tissue culturability'), which is not found in all potato cultivars (Sonnino et al., 1989). A 'monoploid sieve' selects against deleterious recessive alleles, allowing only the genotypes with high fitness values to develop into monoploid plants. These monoploids can be somatically

doubled to produce homozygous diploids for heterosis breeding as described later (Lightbourn and Veilleux, 2007).

2.4 Germplasm Enhancement

2.4.1 Haploid-species hybrids

Haploids (2x) of tetraploid potato cultivars are commonly used to access the germplasm of wild diploid *Solanum* species (Jansky et al., 1990). These haploids readily cross with most diploid *Solanum* species, often producing fertile interspecific hybrids (Hermundstad and Peloquin, 1985a; Yerk and Peloquin, 1989). Wild *Solanum* species require a short critical photoperiod for tuberization, so they produce stolons rather than tubers under the long day conditions of summer in northern temperate regions (Rudorf, 1958). However, when these wild species are crossed to haploids of the cultivated potato, the majority of the resulting hybrids tuberize under long days (Figure 2.4) (Hermundstad and Peloquin, 1986; Yerk and Peloquin, 1989). Haploid–wild species hybrids therefore allow breeders to capture valuable genes from wild species in an adapted form that can be maintained clonally as tubers. Both the haploid parent (Hermundstad and Peloquin, 1986; Yerk and Peloquin, 1989) and the wild species parent (Yerk and Peloquin, 1989) influence the photoperiod adaptation in hybrid families.

It is difficult to evaluate the contribution of wild *Solanum* species for tuber traits such as nutritional quality because they do not tuberize in the field in temperate zone production areas. However, tremendous heterosis for yield is often observed in haploid–wild species hybrids (Leue, 1983; Hermundstad and Peloquin, 1986; Santini et al., 2000). The high yield and large tuber size in hybrids allows breeders to determine the contributions of wild species to tuber traits such as dry matter content, dormancy, starch composition, nutritional components, and processing quality (Yerk and Peloquin, 1989; Janskv et al., 1990; Yerk and Peloquin, 1990a; Serquén and Peloquin, 1996; Rousselle-Bourgeois and Rousselle, 1992; Santini et al., 2000; Oltmans and Novy, 2002; Ortega and Carraso, 2005). Surprisingly, even though half of the genes in these hybrids are from wild species, they exhibit acceptable tuber color, shape and size. In contrast, hybrids between cultivated diploid relatives produce tubers with irregular shape, deep eyes, and short dormancy (De Jong and Tai, 1977). In addition to variation for tuber traits, haploid–wild species hybrids exhibit useful variation for disease resistance and stress tolerance (Watanabe et al., 1995; Carputo et al., 1996; Tucci et al., 1996; Carputo, 2000; Jansky and Rouse, 2000, 2002; Ortega and Carraso, 2005).

Haploid–wild species hybrids are generally male fertile, although fertility varies by wild species parent (Leue, 1983; Hermundstad and Peloquin, 1985b; Yerk and Peloquin, 1988; Tucci et al., 1996). In contrast, when the cultivated diploids from Phureja and Stenotomum Groups are used as male parents in crosses to haploids, their offspring exhibit cytoplasmic-genetic male sterility (Ross et al., 1964; Grun and Aubertin, 1966). Reciprocal crosses, using pollen from haploids,

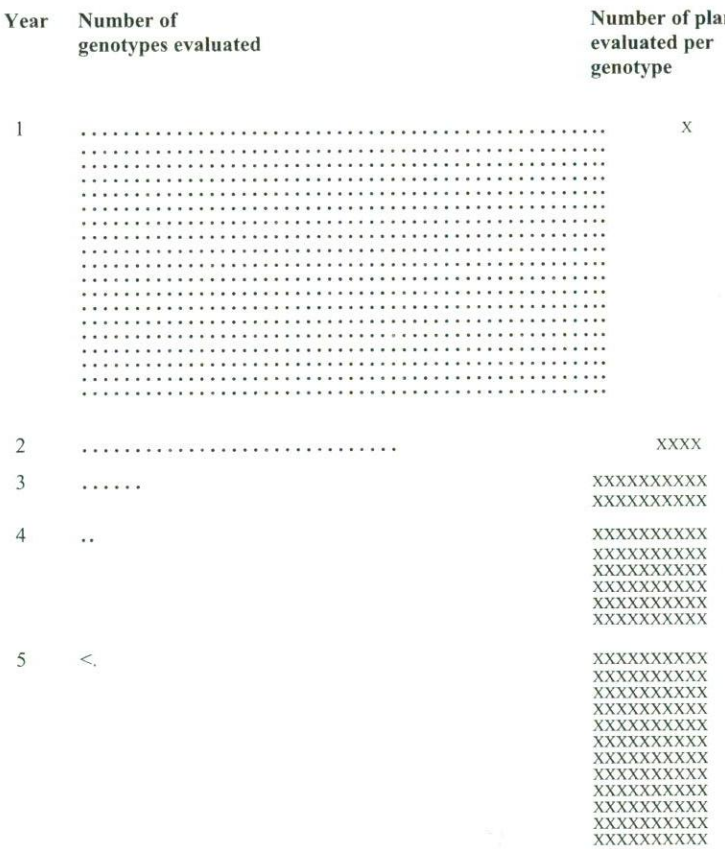

Figure 2.4: Selection intensity in a typical potato breeding program. Each dot represents 100 genotypes. Each x represents a single plant.

produce male fertile hybrids. However, many haploids are male sterile and cannot be used as pollen parents (Peloquin and Hougas, 1960).

2.4.2 Sexual polyploidization

While the development of potato cultivars at the diploid level sounds appealing, it is not likely to be successful. In potato, intralocus (dominance) and interlocus (epistasis) interactions are necessary to maximize yield (Mendoza and Haynes, 1974b). Tetraploidy offers many more opportunities to create such interactions. Two options are available to bring diploid hybrids to the tetraploid level. First, they can be somatically doubled through chemical means such as colchicine (Ross et al., 1967) or through tissue culture (Sonnino et al., 1988). However, tetraploids produced by this method do not exhibit a yield increase, because new interlocus and intralocus interactions are not created (Rowe, 1967; Maris, 1990; Tai, 1997). Somatic doubling

can produce only one type of heterozygote (duplex-AAaa) and a maximum of two alleles per locus. An alternative method to double chromosome number is through sexual polyploidization (Chase, 1963) using 2n gametes. Unilateral sexual polyploidization results from polyploidization of one parent, while the other parent is already at the polyploid level (4x female X 2x male or 2x female X 4x male to produce 4x offspring). Bilateral sexual polyploidization results from polyploidization of both parents (2x X 2x to produce 4x offspring). Triploid offspring are not produced from these crosses due to endosperm failure. Sexual polyploidization can produce three types of heterozygotes (simplex-Aaaa, duplex-AAaa, and triplex-AAAa) and up to four alleles per locus. Complex combinations of triallelic ($A_1A_2A_3A_3$) and tetraallelic ($A_1A_2A_3A_4$) loci can also be produced. In addition, sexual polyploidization produces a wide array of complex epistatic (interlocus) interactions.

Initial studies of sexual polyploidization in potato focused on tuber yield and quality. A high degree of heterosis for yield has been demonstrated following unilateral sexual polyploidization in which the tetraploid female parent is typically a potato cultivar or advanced breeding selection and the diploid male parent is a haploid X wild species hybrid or a cultivated diploid X haploid hybrid (De Jong et al., 1981; Bani-Aameur et al., 1991; Tai and De Jong, 1991; Buso et al., 1999a, 2000, 2003; Alberino et al., 2004). Yield heterosis is realized in 4x X 2x crosses because the diploid parent contributes allelic diversity and 2n gametes transmit a large proportion of heterozygous loci and epistatic interactions to the tetraploid offspring. Another advantage of the USP breeding scheme is that it provides the opportunity to select high-yielding clones with good quality from relatively small segregating populations (Concílio and Peloquin, 1991; Buso et al., 1999b). This is because a much larger proportion of clones from 4x X 2x crosses exhibit high tuber yield and acceptable tuber appearance than from 4x X 4x crosses. Products of unilateral sexual polyploidization also typically exhibit high levels of yield stability across environments, presumably due to the buffering provided by allelic diversity (Darmo and Peloquin, 1990; Ortiz et al., 1991). This is likely to result in more effective selection in early generations of a breeding program.

Recent studies have focused on the use of sexual polyploidization to transfer additional traits, including stress tolerance, processing quality, and disease resistance, to tetraploid offspring. Stable resistance to internal heat necrosis and high specific gravity have been reported in progeny of 4x X 2x crosses (Sterrett et al., 2003). Tetraploids with good chip color and resistance to cold sweetening have been produced via 4x X 2x crosses (De Jong and Tai, 1991; Hutten et al., 1996; Hayes and Thill, 2002a). Unilateral sexual polyploidization has successfully created hybrids with resistance to bacterial wilt (Watanabe et al., 1992), early blight (Herriott et al., 1990), common scab (Murphy et al., 1995), potato cyst nematode (De Maine et al., 1986; Ortiz et al., 1997), Verticillium wilt (Frost et al., 2005), and soft rot (Carputo et al., 2000; Capo et al., 2002). Tetraploids with Colorado potato beetle resistance have been created by crossing tetraploids with diploids containing the cry3Aa transgene (Johnson and Veilleux, 2003; Johnson

et al., 2003). Iwanaga et al. (1989) crossed root knot nematode-resistant diploids to tetraploid 'Atzimba' and to a haploid (2x) of 'Atzimba,' both of which are susceptible to the nematode. A significantly higher proportion of resistant offspring (25%) was obtained in the 4x X 2x crosses than in the 2x X 2x crosses (11%). Presumably, nematode resistance alleles at loci between the centromere and the first crossover on each chromosome were transferred to offspring intact in FDR 2n pollen in the 4x X 2x crosses, but those alleles segregated randomly in the formation of normal pollen in 2x X 2x crosses. This may also explain why 2n gametes transmit resistance to bacterial wilt, root-knot nematodes, late blight, and glandular trichomes to a high proportion of 4x X 2x offspring (Watanabe et al., 1999).

It is interesting that dramatic differences are often observed between 4x (female) X 2x and 2x (female) X 4x crosses. This is presumably because the diploid parent in a 4x X 2x cross produces 2n pollen via a first division restitution mechanism, while that in a 2x X 4x cross produces 2n eggs via a second division restitution mechanism. As discussed above, the genetic consequences of first division restitution mechanism are very different than those of second division restitution. Offspring from 4x X 2x crosses produce higher yields and tuber dry matter content than those from 2x X 4x crosses (Kidane-Mariam and Peloquin, 1974; Hutten et al., 1994). However, there is no difference between the cross types for vine maturity and chip color.

Bilateral sexual polyploidization provides an alternative sexual polyploidization strategy. In this scheme, both parents are diploid and produce 2n gametes. The potential advantage of bilateral sexual polyploidization is that highly heterotic offspring can be produced by crossing diverse diploid parents. The disadvantage is that both parents must produce 2n gametes. In addition, since the meiotic mutations that produce 2n gametes exhibit variable expressivity (n and 2n gametes are produced by the same plant), both diploid and tetraploid offspring will be produced. Tetraploid progeny from bilateral sexual polyploidization are highly heterotic and typically outyield their diploid full-sibs (Mendiburu and Peloquin, 1977; Hutten et al., 1995a) and even tetraploid commercial cultivars (Werner and Peloquin, 1991c). The yield gains from bilateral sexual polyploidization are typically higher than those from unilateral sexual polyploidization, presumably due to the contributions of heterozygosity from both parents (Werner and Peloquin, 1991c).

2.4.3 Polyploidization by somatic fusion

The cultivated potato and many of its relatives are amenable to cell and tissue culture procedures, including protoplast isolation and fusion. Somatic cell fusions have frequently been used to combine the genomes of *Solanum* species that are sexually incompatible because of pollen–stylar interactions or mismatched EBN numbers. Somatic fusion circumvents sexual reproduction and results in novel combinations of not only nuclear genomes, but also cytoplasmic genomes (Trabelsi et al., 2005; Bidani et al., 2007; Lovene et al., 2007). However, recalcitrant genotypes

are common, so some combinations can not be made. In addition, genetic recombination may not occur in some somatic hybrids, limiting introgression of foreign genes.

A common somatic fusion strategy fuses protoplasts of tetraploid cultivars with those of sexually incompatible diploid wild species. The resulting hexaploid hybrids are often fertile and crossable with the tetraploid cultivars (Austin et al., 1987; Fish et al., 1988; Helgeson et al., 1988; Carputo, 1997; Helgeson et al., 1998). The pentaploid offspring are also fertile and tetraploid clones are recovered after a few backcrosses. Alternatively, diploid cultivated potato clones can be fused with diploid wild species to produce tetraploid hybrids (Rokka et al., 1994; Carputo, 1997; Przetakiewicz et al., 2007). However, hexaploid somatic hybrids from 4x + 2x fusions are typically more successful in crosses to cultivars than are tetraploid hybrids from 2x + 2x fusions (Helgeson et al., 1988). Most somatic fusions have been carried out to capture disease resistance genes, but somatic fusion hybrids with improved salt tolerance have also been developed (Bidani et al., 2007). While chromosomes from both parents are typically found in somatic fusion hybrids, the genetic contributions of some wild species are lost more rapidly than others in backcross generations (Naess, 2001).

Another application of somatic fusion is to combine disease resistance genes from two sexually compatible parents. When protoplasts of diploids carrying a major gene for PVX resistance (Hines and Marx, 2001) were fused with those of diploids carrying a major gene for PVY resistance (*Ry*), most of the hybrids expressed both genes (Thach, 1993). Similarly, when clones carrying genes for resistance to different pathotypes of potato cyst nematode were fused, some of the hybrids were resistant to both pathotypes (Rasmussen, 1996). Foliar and tuber late blight resistance have also been combined in somatic fusion hybrids (Rasmussen et al., 1998). The fusion of diploid *S. verrucosum* protoplasts with those of cultivated potato clones combined PLRV resistance from *S. verrucosum* with adaptation and tuber yield from the cultivated potato donor (Carrasco, 2000).

Sometimes levels of resistance are not as high in somatic fusion hybrids as in the donor clones, presumably due to a dilution effect in the polyploid hybrids (Cooper-Bland, 1994; Rasmussen et al., 1998; Carputo et al., 2000b; McGrath, 2002; Gavrilenko, 2003). On the other hand, somatic hybrids produced from fusions of cultivated potato with the wild species *S. nigrum* were often more resistant than the resistant wild parent, perhaps due to complementation of resistance genes (Zimnoch-Guzowska, 2003).

2.5 Genetics

2.5.1 Polyploid versus diploid genetics

The cultivated potato is considered to be an autopolyploid because its subgenomes are similar. All four sets of chromosomes are capable of pairing with each other, so trivalents and

quadrivalents are observed in early stages of meiosis. A trivalent is an association of three homologous chromosomes in early stages of meiosis, while a quadrivalent is an association of four homologous chromosomes. Consequently, the cultivated tetraploid potato exhibits tetrasomic inheritance (Howard, 1970; Ross, 1986; Hawkes, 1990). Tetraploid potato cultivars are described as $2n = 4x = 48$, meaning that the sporophyte generation (2n) contains four sets of chromosomes (4x) and there are 48 chromosomes in each somatic cell. Gametes from a cultivar are $n = 2x = 24$. In this case, 'n' refers to the gametophyte generation.

Three types of gene segregation occur in autotetraploids (Little, 1945; Little, 1952; Burnham, 1962). The type of segregation depends on the location of the gene relative to the centromere. If a gene is close to the centromere, then a crossover between that gene and the centromere is unlikely to occur and that gene will experience chromosome segregation. That is, the gene segregates with the chromosome on which it resides. Consequently, a triplex (AAAa) genotype will produce 50% AA and 50% Aa gametes. Notice that no aa gametes are produced. In the other two types of segregation, called random chromatid segregation and maximum equational segregation, the gene is far enough from the centromere that a crossover can occur during meiosis. Consequently, it is possible for the sister chromatids carrying the recessive allele to end up in the same gamete (aa) through a process called double reduction. Four requirements must be met to achieve double reduction: (1) A quadrivalent must form. That is, all four homologous chromosomes must associate with each other through crossing-over at meiosis. (2) Crossing-over must occur between the gene of interest and the centromere. (3) The two pairs of chromosomes that were involved in the crossover must end up at the same pole after the first meiotic division. (4) Chromatids must separate randomly during the second meiotic division. If these criteria are always met, then maximal equational separation occurs and the frequency of double reduction is 1/6. A less extreme type of segregation occurs when chromatids segregate randomly, resulting in 4/28 or 1/7 gametes carrying sister chromatids. Consequently, random chromatid segregation results in a frequency of double reduction of 1/7. It does not require a crossover between the gene and the centromere in every meiotic cell. With random chromatid segregation, all combinations of chromatids must be considered when determining gametic ratios. The gametes produced by a triplex (AAAa) individual would be all pairwise combinations of AAAAAAaa, which would be 15 AA, 12 Aa, and 1 aa, or 27 with the dominant genotype and one with the recessive genotype.

Two points should be emphasized regarding segregation ratios in polyploids with tetrasomic inheritance. First, the segregation ratio of a particular gene depends on its location on the chromosome. This is in contrast to diploid segregation ratios, which do not depend on a gene's chromosomal position. Second, large samples of segregating populations must be evaluated in order to characterize genetic ratios and to identify clones carrying genes for improved quality and disease resistance (Little, 1945). For example, it is necessary to evaluate at least 1700 plants to distinguish between chromosome segregation and random chromatid segregation when selfing a duplex clone. Consequently, genetic analysis at the tetraploid level is difficult. Segregation

ratios are not clearly delineated because they depend on the crossover frequency between the gene and the centromere, which may be environmentally variable. Consequently, statistical analyses are difficult to perform. Fixed ratios can be predicted from chromosome and random chromatid segregation models. However, they represent extremes. In reality, these extremes are rarely attained and ratios fall between them. Exact ratios can not be predicted because they are determined by crossover events, which differ in every meiotic cell. In addition, epistatic (interlocus) interactions are magnified in tetrasomic tetraploids, gene dosage effects are often important, and interactions with the environment can be complex. All of these complications result in a loss of resolution at the tetraploid level, so that qualitative traits are difficult to identify.

Historically, genetic studies in potato have been based on tetraploid families. As mentioned above, even major genes are difficult to identify at the tetraploid level due to the complexities of tetrasomic segregation. For example, Brown et al. (1997) intercrossed tetraploid cultivated potato clones and obtained high heritability estimates for potato leaf roll virus resistance. A few major genes are likely to be mainly responsible for resistance, but it was not possible to identify individual genes and their effects. In contrast, when Brown and Thomas (1994) carried out inheritance studies at the diploid level, with the wild species *S. chacoense*, a single dominant resistance gene was identified and parental genotypes were determined based on standard diploid segregation ratios.

Even highly selected tetraploid potato clones contain undesirable alleles along with desirable ones. The proportion of deleterious alleles in a plant is called the genetic load. Most deleterious alleles are recessive, so they are only expressed when homozygous. Consequently, the genetic load is high in tetraploids where homozygous recessive genotypes are less common than in diploids. These deleterious alleles are hidden by dominant alleles in tetraploid clones and do not typically have a negative effect. However, when tetraploid clones are self-pollinated or crossed to related clones, some of their offspring will be homozygous for deleterious recessive alleles and will exhibit reduced vigor and/or fertility. These clones are discarded as seedlings in breeding programs. Therefore, one method to measure the genetic load in parents used in breeding programs is to self them and measure the proportion of non-vigorous offspring. It may be beneficial to select parents, in part, based on low genetic load.

Gene expression was studied in a 1x, 2x, 4x polyploid series created by somatic doubling (Stupar et al., 2007). It is interesting that a linear correlation between gene expression and ploidy was rarely found. That is, the diploid and tetraploid clones exhibited similar gene expression patterns. The diploid plants in this study were actually more vigorous than the tetraploid ones. The cost to maintain more DNA and larger cells was apparently not compensated by higher gene expression. The tetraploids in this study were produced by somatic doubling, so they were not able to exploit the heterozygosity necessary for enhanced fitness in polyploids.

2.5.2 *Major genes for economically important traits*

Many genetic studies in potato have focused on disease resistance. A summary of disease resistance genes and quantitative trait loci in potato has recently been published (Celebi-Toprak et al., 2005b). In addition, major quantitative trait loci have been identified for tuber dormancy (chromosome II), tuber eye depth (chromosome X), flesh color (chromosome IV), tuber shape (chromosome II) and uniformity of tuber shape (chromosome III) (Sliwka et al., 2008).

Another important trait is pigment production, because it determines skin and flesh color. In 1911, Salaman indicated that, in tetraploid potato, the dominant allele of gene *D* is needed for coloration in the skin. Later, the dominant allele of gene *I* was reported to be necessary for skin coloration in diploid potatoes (Dodds and Long, 1956). Genes *D* and *I* are the same, so gene *D* will be used for the remainder of this discussion. Therefore, all *dd* genotypes lack pigmentation and produced white-skinned tubers. Genotypes with the *D* allele are red if they carry the dominant *R* allele and are homozygous recessive for the *P* gene (D-R-pp) (Dodds and Long, 1955). They are purple if they carry the dominant *P* allele, regardless of the genotype at the *R* gene (D—P-). The production of pelargonidin-based (red) anthocyanin pigments in plants requires the activity of dihydroflavonol 4-reductase (DFR), which is encoded by gene *R* (De Jong et al., 2003). The red allele of gene *R* is predicted to encode a 382-amino-acid protein that differs at ten amino acid positions from the gene products of alternative alleles. It is interesting to note that DNA sequence data from this study support the hypothesis that *R* was selected once during the domestication of the potato (Dodds and Long, 1955). The *P* locus codes for flavonoid 3',5'-hydroxylase, resulting in purple pigmentation (Jung et al., 2005). The production of anthocyanins in tuber flesh requires the dominant *Pf* gene, along with the *R* and *P* genes described above (De Jong, 1987) Genes *D* and *Pf* are closely linked (De Jong, 1987). The production of carotenoid pigments (yellow) in tuber flesh requires the dominant *Y* gene (Fruwirth, 1912). Russet skin is apparently controlled by three dominant genes, but the genetic system has not been clearly elucidated (De Jong, 1981).

An understanding of the genetic basis of the photoperiod response for tuberization would help geneticists and breeders to maximize their use of wild species germplasm. A two-gene model duplicate dominant epistasis model has been proposed for the control of tuberization under long-day conditions (Jansky et al., 2004). Clones with at least one dominant allele of one or two genes tuberize in temperate regions. In this model, wild species are homozygous recessive for both genes. Modifier genes are presumed to influence minor variability in the tuberization response.

Major genes also appear to control resistance to cold sweetening, an important processing trait. A three-gene model has been proposed for good potato chip quality when tubers are used directly out of cold storage (Thill and Peloquin, 1994). Another three-gene model explains chip quality when tubers are reconditioned prior to processing. There may be some overlap in these genes.

Acid invertase and UDP-glucose phosphorylase appear to be especially important components of the carbohydrate metabolism pathway as it relates to the accumulation of reducing sugars. Alleles associated with both enzymes have been found to be associated with resistance to cold sweetening (Sowokinos et al., 1997; Sowokinos, 2001; Li et al., 2005; McKenzie et al., 2005).

2.6 Cultivar Development

2.6.1 Choice of parents

A potato breeder's most important decision is which parents to use in crosses. Based on experience, breeders choose parents and parental combinations that result in a relatively high proportion of desirable offspring. Predictions of parental value can be obtained by visually scoring tubers of several families involving the same parent (Brown and Dale, 1998). In addition to specific parental combinations, the proportion of desirable phenotypes in a hybrid family depends on the cross type being evaluated. For example, a breeder is likely to select a higher proportion of clones from a cross between two white parents than from a cross between two red clones because the red family will contain a high proportion of clones with unacceptable skin color. That breeder will select an even lower proportion of clones from crosses between long, russet clones because both round and lightly russeted clones will be discarded. Typically, breeders will maintain separate sets of parents for each market type (red, white, russet). Crosses within market types are more common than across market types. When breeders find that they need to move toward a new market use, they typically make progress toward that goal by choosing appropriate genetically diverse parents. For example, when the U.S. processing industry began to expand dramatically in the mid-20th century, breeders responded by selecting for high dry matter content and chip color. Chip cultivars released in recent decades are far superior to previously released cultivars (Douches et al., 1996).

Genetic variance for yield in potato is mainly non-additive, involving intralocus and interlocus interactions (Mendoza and Haynes, 1974b; Tai, 1976). The genotypic value of a parental clone can be partitioned into additive, dominant, and epistatic contributions to its offspring. The additive component is due to alleles that contribute a fixed value to the genotype. It is the portion of an individual's breeding value that is passed on to offspring. The dominance component is composed of interactions between dominant and recessive alleles at a locus. In diploid populations, the dominance component of variance can not be passed on to offspring because it is lost when meiosis generates haploid gametes. Similarly, interactions among genes (epistatic interactions) are not transmitted intact to the next generation in diploid crosses. Of course, since tetraploids produce diploid gametes, they can pass complex combinations of genes and alleles on to their offspring. Quantitative genetic analyses in tetraploid breeding populations have shown that non-additive genetic variance is important for most economically important traits, including yield, specific gravity (dry matter content), tuber size, and tuber number (Killick, 1977). Consequently, selection can not be carried out on parental clones alone because parental

performance can not be used to predict progeny means, even if parental performance is known from other crosses. Therefore, one option is to make trial crosses of all parental combinations, grow out small families for evaluation, and then grow out larger samples of the best families. Another option is to measure the mean performance of progenies developed by selfing, which can provide some measure of prediction of progeny means of crosses (Gopal, 1998). Evaluations of families developed by selfing will also provide an approximation of the genetic load carried by each parent, which may impact parental value.

In potato, because non-additive (dominance and epistatic) genetic effects are so important for economically important traits, strategies have been developed to allow superior parents to transmit more than their additive genetic component to their offspring. In fact, 2n gametes are able to pass along intact groups of alleles retaining epistatic and dominance interactions. Major loci for tuber yield in potato are located in the chromosome regions between centromeres and proximal crossovers (Buso et al., 1999c). Transmission of heterozygosity associated with yield, then, is especially effective using FDR 2n gametes of potato.

2.6.2 Breeding strategies

Conventional potato breeding involves the intercrossing of heterozygous tetraploid clones (Bradshaw and MacKay, 1994). Segregation results in a very low percentage of desirable genotypes. Often, highly selected but genetically related parents are intercrossed, limiting breeding progress for both yield and yield stability (Mendoza and Haynes, 1974a) because potato exhibits severe inbreeding depression (De Jong and Rowe, 1971; Birhman and Hosaka, 2000). In a typical breeding program, up to 100 000 (and sometimes more) seedlings are grown from crosses between dozens of parents (Figure 2.4). A single tuber is collected from each plant in each family to create a family bag. These tubers are planted in the field as single 'hills' (plants). Selection is then carried out on single hills, mainly for tuber appearance and, to some extent yield and size. Selection pressure is very high at this stage, typically with less than 1% of the clones retained. Selection pressure is higher in some families than others, depending on breeding goals and phenotypic variability. In successive years, the number of genotypes planted decreases while the number of hills evaluated per genotype increases. It is important to evaluate advanced selections across multiple years and production environments to measure performance stability. Consequently, 10 or more years of evaluation are required before a clone is considered for cultivar status.

The phenotype of a potato plant is very plastic (environmentally variable) with regard to many traits of interest for potato breeders. The effect of production environment on traits such as yield, tuber number, tuber size, specific gravity, and processing quality presents a challenge that is difficult to overcome. It requires the testing of clones in multiple years and locations. For example, quantitative trait loci have been detected for tuber starch content, but few were stable across environments (Schäfer-Pregl et al., 1998). Similarly, environment has a large impact on

chip color and its components (Tai and Coleman, 1999; Blenkinsop et al., 2002; Hayes and Thill, 2003). In addition, levels of nutritional compounds, such as antioxidants and vitamins, vary with production environment (Hamouz et al., 1999; El-Morsi et al., 2000; Reyes et al., 2004; Rosenthal and Jansky, 2008). In a study on flavor components in baked potatoes, production and storage environments were found to be major sources of variation (Jansky, 2008).

Potato exhibits strong hybrid vigor due to genetic interactions within and among loci (Tai, 1976). Because high potato yield and vigor depend on interlocus and intralocus interactions, breeding strategies typically aim to maximize heterosis. The most extreme heterosis breeding strategy is to develop highly inbred clones at the diploid level and then combine genetically diverse diploids to produce heterotic hybrids. One heterosis breeding strategy creates a genetically diverse set of doubled monoploids and then somatically hybridizes them to create highly heterozygous diploids. This method has been attempted using diploid cultivated clones (Lightbourn and Veilleux, 2007). A number of roadblocks have limited the success of this first attempt to create heterotic diploids. These included genotypes that did not respond to anther culture, weak monoploids, the fixation of undesirable tuber quality traits, and polyploid somatic fusion hybrids. The monoploid sieve in this case may have been too dramatic, eliminating epistatic and intra-allelic interactions that were present in the heterozygous diploid donors. It is possible that some alleles that were valuable in a heterozygous condition were eliminated during the monoploid sieve.

Another option is to create homozygous diploids using self-incompatibility inhibitors to allow self-pollination (Birhman and Hosaka, 2000). This allows for the development of clones with fixed (homozygous) genes for traits of interest. Highly homozygous inbreds could also be used for heterosis breeding. Each generation of self-fertilization reduces heterozygosity by 50%. This rate of approach to homozygosity may be too high in potato, where inbreeding depression results in dramatic reductions in fertility and plant vigor (Phumichai et al., 2005; Phumichai and Hosaka, 2006). Sib-mating is an attractive alternative that provides a smoother transition to homozygosity.

Unilateral sexual polyploidization offers a modified form of conventional breeding that can maximize the effects of heterosis. Exceptionally high tuber yields have been observed in tetraploid ($2n = 4x = 48$) progenies obtained from 4x X 2x matings in potatoes (Hanneman 1968; Hanneman and Peloquin 1969; Kidane-Mariam and Peloquin 1972; Mok and Peloquin 1975a; Jansky and Peloquin, 2006). The progeny of 4x X 2x crosses are typically vigorous and relatively uniform for high tuber yield, which may at first seem surprising, considering the heterozygosity of the parents. The heterotic response is most commonly observed when the tetraploid is used as the female parent and the diploid parent produces 2n pollen by a first division restitution mechanism. In addition, families from 4x X 2x (first division restitution 2n pollen) crosses outyield 4x X 2x (second division restitution 2n pollen) and 4x X 4x families by about 50% (Mok and Peloquin, 1975b). Because intralocus and interlocus interactions contribute to high

yield in potato, this significant increase in yield by 4x X 2x (first division restitution pollen) hybridization is most likely due to the increase in transmission of heterozygosity and epistasis by 2n first division restitution gametes (Mendiburu and Peloquin 1977). However, high tuber yield must be accompanied by acceptable tuber quality. Schroeder (1983) reported that a large number of haploid (2x) X diploid *S. chacoense* hybrids used in USP schemes produced tetraploid offspring with good tuber appearance and size, along with high yield. Similarly, Buso et al. (1999) identified families from crosses between tetraploids and 2x haploid X *S. chacoense* hybrids with general tuber appearance scores similar to commercial cultivars.

2.6.3 Early generation selection

Most potato breeding programs evaluate tens of thousands of seedling genotypes every year. It is not unusual to discard over 99% of those plants based on visual appearance of tubers. In later generations, after the number of genotypes has been reduced considerably, breeders select for disease resistance and tuber quality in replicated plots with multiple hills (plants) of each clone (Louwes and Neele, 1987). However, early generation selection would allow breeders to retain superior genotypes before the population size has been dramatically reduced and while genetic variability is high (Caligari et al., 1986). Selection for tuber appearance in early generations enhances genetic gains for yield (da Silva et al., 2006). Significant genetic gains in chip potato populations were also reported when seedlings were selected for low glucose levels based on greenhouse-grown minitubers or in vitro grown microtubers (Xiong et al., 2002). In addition, specific gravity of field-grown tubers was found to be associated with that of minitubers and microtubers. It is often difficult to carry out severe selection for tuber quality traits and yield components in early generations, though, because they are strongly influenced by environment (Anderson and Howard, 1981; Brown et al., 1987; Love et al., 1997; da Silva et al., 2006). For example, early generation selection for resistance to cold sweetening is somewhat effective, but its efficiency is reduced by environmental effects on chip color (Thill and Peloquin, 1995; Hayes and Thill, 2002b; Hayes and Thill, 2003). Instead, a more moderate selection intensity or negative selection (eliminating clones with poor performance) is likely to be more effective (Tai and Young, 1984; Maris, 1988; Gopal et al., 1992; Love et al., 1997).

2.6.4 Marker-assisted selection

Some molecular markers associated with major genes are available for use by potato breeders, mainly for disease resistance traits. They include markers for resistance to late blight, potato virus X, potato virus Y, potato virus A, potato virus S, potato cyst nematode, potato root knot nematode, and soft rot (reviewed by Celebi-Toprak et al., 2005a). Recently, molecular markers for resistance to Verticillium wilt have also been identified (Simko, 2004; Simko et al., 2004a, b; Bae et al., 2008). Specific alleles for genes that control the carbohydrate pathway have been found to be associated with resistance to cold sweetening (Sowokinos et al., 1997; Sowokinos, 2001; Li et al., 2005). A marker associated with the gene for sucrose synthase has been found

to be effective in selecting for clones with light chip color (Kawchuk et al., 2008). Historically, markers have been developed using a genetic mapping approach, in which the trait of interest is genetically linked to the marker. This approach requires the development of a fine map in order to prevent recombination between the marker and the gene of interest. Markers based on candidate genes for the traits of interest are not influenced by recombination and are becoming more common as studies elucidate the molecular basis of disease resistance and quality traits. A number of quantitative trait loci have also been identified in potato for both disease resistance and agronomic traits such as starch content, protein storage, and glycoalkaloid production (reviewed by Celebi-Toprak et al., 2005a).

2.6.5 Traits of interest

Historically, breeders have focused on yield, tuber quality, and disease resistance during cultivar development. Progress toward the development of disease-resistant cultivars has recently been reviewed so this topic will not be considered here (Jansky, 2000). A complex set of external and internal quality traits is required for fresh market and processed potatoes. External quality traits include tuber size and shape, eye depth, skin color, and lack of blemishes due to bruising and disease. These traits are especially important for fresh market potatoes, but they may also impact processing quality. Internal quality includes dry matter content, nutritional quality, flavor, starch quantity and quality, and lack of defects such as hollow heart and internal necrosis. In recent years, breeders have been increasingly interested in improved nutritional quality and flavor. Since consumers in many countries eat potatoes more frequently and in larger quantities than other vegetables, any improvement in nutritional composition is likely to result in significant health benefits. Consequently, there is considerable potential to develop the potato as a functional food with health-promoting or disease-preventing properties beyond the basic function of supplying nutrients. These traits require complex chemical analyses and sometimes sensory evaluations, which currently limit the ability of breeders to identify superior phenotypes. A sample of quality traits is discussed below.

1. **Specific gravity**. Tuber specific gravity, which is a measure of dry matter content, is a critical processing quality trait. Cultivars with high dry matter are required for the production of fries, chips, and starch. The genotype–environment interaction for specific gravity is generally low, so rankings of cultivars do not change across years and production environments (Killick and Simmonds, 1974). Heritabilities are moderate to high, allowing for genetic gains to be made by selecting clones with high specific gravity (Killick, 1977; Tai, 1976; Haynes et al., 1989). High specific gravity is often noted in tetraploid clones derived from sexual polyploidization in which the diploid parent contains wild or cultivated potato relatives (Tai and De Jong, 1991; Ortiz et al., 1997; Buso et al., 2000).

2. **Ascorbic acid**. The potato is a significant dietary source of ascorbic acid (vitamin C), which is necessary for normal collagen formation and which acts as an antioxidant. In

addition, ascorbic acid inhibits enzymatic browning of tuber flesh, preventing a significant problem for the potato-processing industry (Finlay et al., 2003). Concentrations in cultivars range from 11 to 36 mg per 100 g tuber tissue (Dale et al., 2003; Love et al., 2003). The U.S.-recommended daily allowance is 60 mg. Ascorbic acid levels decrease over time in storage, but genotypic differences in the ability to maintain ascorbic acid levels during storage have been reported (Davies et al., 2002; Finlay et al., 2003). This quality is important because many potatoes are consumed after a storage period.

3. **Antioxidant capacity**. There is currently considerable interest in the nutritional value of antioxidants in vegetable crops. Carotenoid and phenolic compounds in potato are potent antioxidants (Brown, 2005). Major genes for carotenoid and flavonoid production have been identified in potato (De Jong, 1991; Van Eck et al., 1994). Carotenoid content increases exponentially with intensity of yellow flesh color (Lu et al., 2001), so it is easy to visually select for improved nutritional quality due to carotenoids. Anthocyanins are responsible for purple and red colors, and can be found at high enough levels to consider potato tubers as sources of natural dyes (Jansen and Flamme, 2006). The antioxidants in colored-flesh potatoes also contribute to potato disease resistance (Wegener and Jansen, 2007). High antioxidant capacity has been reported in white-fleshed potatoes, indicating that colorless flavonoids or phenolics may also be important (Hale, 2003). Antioxidant levels are strongly influenced by production environment and storage conditions (Reyes et al., 2004; Rosenthal and Jansky, 2008). Consequently, it is important to distinguish between genotypic and environmental sources of variation when breeding for enhance antioxidant capacity.

4. **Enhanced flavor**. Flavor is due to the combination of taste, aroma, and texture. Raw potatoes are bland, but become more flavorful when heated, as a result of chemical changes (Maga, 1994). Although potatoes are not considered to have a strong flavor, the components of flavor are complex (Coleman et al., 1981). Pyrazines are considered to be among the most important and characteristic components of baked potato flavor (Buttery et al., 1973). They are produced by the non-enzymatic Maillard reaction, in which sugars interact with amino acids at high temperatures. There is a strong positive relationship between pyrazines and organoleptic quality in both baked potatoes (Maga and Holm, 1992) and potato chips (Maga and Sizer, 1973). The breakdown products of RNA, 5' ribonucleotides, act as precursors for flavor enhancers called umami compounds. Steamed or boiled tubers of landrace cultivars with higher levels of glutamate and guanosine 5'-monophosphate (GMP) than *S. tuberosum* cultivars had higher acceptability scores in taste tests (Morris et al., 2007). The most important ribonucleotides for flavor enhancement are inosine 5'-monophosphate (Marcel et al., 2003) and GMP. They are present in low quantities in raw potatoes, but levels increase during cooking as RNA is degraded. Both levels and types of ribonucleotides vary among potato cultivars (Maga and

McNeill, 1986). This is probably due to differences in the activities and types of enzymes that break down RNA. A synergistic effect is detected when 5' ribonucleotides interact with amino acids, especially glutamate.

5. **Resistance to cold sweetening**. Most potato tubers are stored for a period of time before they are processed. When they are stored at low temperatures (<10°C) to prevent losses due to shrinkage and disease and to prevent sprouting, they undergo a phenomenon called low-temperature sweetening. This results primarily from the accumulation of reducing sugars (glucose and fructose) as starch breaks down. These sugars interact with amino acids in the Maillard reaction, causing unacceptably dark fried products (Coffin et al., 1987). It is often possible to reduce the effects of low temperature storage by reconditioning the cold-stored tubers at warmer temperatures prior to processing. This causes some of the sugars to be converted back into starch. However, reconditioning is not always effective (Coffin et al., 1987). Using wild *Solanum* relatives, however, breeders have been able to improve levels of resistance to cold sweetening in breeding clones and cultivars (Thill and Peloquin, 1994; Hayes and Thill, 2002a, c; Domanski et al., 2004; Hamernik et al., 2009). Quantitative trait loci have been identified which are linked to genes encoding enzymes in carbohydrate metabolic pathways (invertase, sucrose synthase 3, sucrose phosphate synthase, ADP-glucose pyrophosphorylase, sucrose transporter 1, and a putative sucrose sensor) (Menendez et al., 2002). It is interesting to note that most QTLs for glucose content mapped to the same positions as those for fructose content. Recent consumer concern about acrylamide levels in fried potato products may be alleviated by breeding for low levels of reducing sugars. Acrylamides result from the interactions of asparagine and reducing sugars during the Maillard reaction. The reducing sugar concentration is the limiting factor in this reaction, so minimizing reducing sugars in tubers is expected to reduce levels of acrylamides in finished products (Silva and Simon, 2005). Selection of cultivars with low levels of acrylamide precursors can alleviate concern about potatoes as significant sources of acrylamides (Vivanti et al., 2006).

6. **Starch content and quality**. Dry matter content in potato tubers is determined in large part by starch content. Starch content is especially important for the processing industry, but it is also of interest in fresh market potatoes because it influences texture. Early maturing cultivars typically do not produce as much dry matter as late maturing clones, which have more time to accumulate photosynthate. As expected, tuber starch content appears to be a polygenic trait. Quantitative trait loci influencing starch content have been identified on each of the 12 chromosomes of potato (Chen et al., 2001; Gebhardt et al., 2005). There is currently interest in breeding for increased levels of amylose in potato starch because high amylose starch has superior nutritional qualities. Following cooking, a portion of high amylose starch recrystallizes to form so-called resistant starch, which acts as a form of dietary fiber (Karlsson et al., 2007). In a survey of wild *Solanum* species,

a large amount of variability was found for dry matter content, starch content, protein content, percent amylose in starch, and the diameter of starch granules (Jansen et al., 2001). These wild species can be introgressed into the cultivated potato as described above, providing the means to improve important tuber quality traits.

2.7 Conclusions

Potato breeders are challenged by the tetraploid nature of the potato, limited variability for economically important traits in adapted breeding clones, and a complex set of requirements necessary for the successful adoption of new cultivars. However, they are fortunate to have access to rich germplasm resources. These resources are readily available in gene banks and the genetic diversity in *Solanum* relatives is typically easily transferred to cultivated potatoes via interspecific crosses. Since the majority of species are 2x (2EBN), the production of haploid–wild species hybrids offers an easy and effective method for capturing much of the diversity in wild *Solanum* species, while allowing breeding and genetic studies to be carried out at the diploid level. Unilateral or bilateral sexual polyploidization can then be used to transfer valuable wild species traits and genetic diversity back to the tetraploid level, where hybrids to cultivars are readily produced. To date, breeders have tapped into only a small fraction of the available genetic resources of potato using these methods. There is good reason for optimism about the prospects for continued genetic improvements in potato. The germplasm resources are abundant in genetic diversity, and breeders have access to a well-stocked toolbox for the utilization of those resources.

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